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# The appendicular muscles of *Necturus maculosus*.

By

**Harris Hawthorne Wilder,**

Professor of Zoology in Smith College, Northampton, Mass., U. S. A.

With 5 Plates.

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*Life Sci* The appendicular muscles of *Necturus maculosus*.

By

**Harris Hawthorne Wilder,**

Professor of Zoology in Smith College, Northampton, Mass., U. S. A.

With Plates 23—27.

*L. Q. Adams 1.00*  
Problems relating to the origin of the hand type of Vertebrate-limb (Chiridium), especially that of its separate parts, are rendered extremely difficult from the outset through the failure of the usual records upon which we are accustomed to rely; the adult anatomy of the lower forms, and the earlier developmental stages in the higher. The earlier forms of Vertebrates with a chiridial appendage have been entirely lost, and thus far, with the exception of a few slight indications, palaeontology is equally silent in the matter. Nor does embryology furnish much more, for it is well-known that, owing to the greatly accelerated development of these parts in all the higher Vertebrates, the earlier stages are either dropped out altogether or are hastened over so rapidly, and with so little attention to details that the cells of which the limb-buds are composed are seen to arrange themselves from the outset into the form of the adult organs, and give few indications of the earlier conditions. It becomes thus of the greatest importance to investigate carefully and put on record the anatomical details of the adult limbs in the lowest tetrapod Vertebrates we still possess, and in this connection the lower Urodeles are seen to be of first importance. Here again, however, the fate investing the early history of the



chiridium is seen to continue, since of the few living representatives of the group, every one has suffered some modification of the free limbs, usually in the form of reduction. Thus *Proteus* and *Amphiuma* have, in some cases two, in others three digits; *Siren* has lost the posterior limbs entirely, and *Necturus* has but four digits on each foot, instead of five, generally supposed to be the typical number. *Cryptobranchus*, long the favorite of the investigator because of its large size and the usual pentadactylous condition of the hind feet, is naturally higher than any Perennibranch and may not be supposed to show a much more primitive condition than one of the higher salamanders.

Our best choice would thus seem to be *Necturus*, in spite of the apparent loss of a digit, since this animal would presumably show more primitive relationships than would any Derotreme, and in the number of its toes more nearly approaches the number assumed to be the normal one than any other Perennibranch. In addition to this, the exact correspondence of the two free limbs in the matter of skeleton leads one to hope that this correspondence may extend also to the other parts, the muscles especially, and thus furnish the ground upon which a scientific serial homology may be based.

It is with these points of theoretical importance in mind that the investigation here presented was undertaken, and it is hoped that the written and pictured description of this, our earliest available tetrapod, may be of value in many questions of comparative myology. One thing becomes at least clear, and that is, the cumbersomeness of our present nomenclature in giving two distinct names to parts clearly the same, as in the case of the majority of the muscles of the free limb. That the most of these differences, like Humero-metacarpalis vs. Femoro-metatarsalis, or Extensor radialis vs. Extensor tibialis, are due to a keeping up of the double nomenclature of the skeletal parts strengthens the appeal for a rationalizing of the terms, at least upon such safe grounds as carpus and tarsus, where the homology is sure.

The difficulties of our present nomenclature are constantly apparent, and in cases where the two limbs are compared the results are often extremely cumbersome. As an illustration of the present necessary mode of expression where comparisons of this nature are dealt with I may cite the opening sentence from a paper on the arteries of the hand and foot (BAUM, in: Anat. Anz., Vol. 31, p. 428), in which the result is wholly the fault of the nomenclature,

as the author could express his ideas in no better way: „Die zur Versorgung der Hand (des Vorderfusses der Tiere) und des Fusses (des Hinterfusses der Tiere) bestimmten Arterien zeigen bekanntlich eine charakteristische Anordnung insofern, als sowohl an der dorsalen, wie volaren (plantaren) Seite des Metacarpus und Metatarsus entsprechend den Interstitien zwischen den einzelnen Metacarpal- (bezw. Metatarsal-) Knochen Arterien herablaufen, die sich dann an den Metacarpo- (bezw. Metatarso-) Phalangealgelenken oder in deren Nähe je in zwei für die einander zugekehrten Flächen zweier benachbarter Finger (Zehen) bestimmte Aeste teilen.“

Of course one must be very sure of homologies before attempting to reform the nomenclature upon that basis, and thus our only hope of relief is through anatomical investigation, collecting and recording all the available facts upon which a scientific nomenclature may be founded. Among such the myology of all types of Urodeles would appear to be of first importance, as presenting conditions the most primitive of any now available.

The muscles treated in this paper include both those of the girdles and the free limbs, and are as follows:

#### A. Muscles between the trunk (or head) and the shoulder-girdle.

##### 1. Dorso-lateral aspect

- Latissimus dorsi (*ld*)
- Dorsalis scapulae (*ds*)
- Omohyoideus (*oh*)
- Trapezius (*t*)
- Levator anguli scapulae (*ls*)
- Serratus anterior (*sa*)

##### 2. Ventral aspect.

- Pectoralis (*p*)

#### B. Muscles between the shoulder-girdle and the free limb.

- Supracoracoideus (*sc*)
- Procoracohumeralis (*ph*)
- Rectus superficialis hypobranchialis posterior (*rh<sub>p</sub>*)
- Anconeus (= Triceps)
- Anconeus scapularis (*ac*)
- Anconeus humeralis lateralis (*ahl*)
- Anconeus humeralis medialis (*ahm*)
- Anconeus coracoideus (*ac*)

Coracobrachialis longus (*cbl*)

Coracobrachialis brevis (*cbb*)

Scapulohumeralis (*sh*)

Humeroantebrachialis (*ha*)

C. Muscles of the distal portion of the anterior limb.

1. Dorsal aspect of forearm and hand.

Humerometacarpalis (*hm*, *hm'*)

Extensor radialis (*er*)

Extensor radialis superficialis (*ers*)

Extensor radialis profundus (*erp*)

Supinator (*s*)

Extensor ulnaris (*eu*)

Extensores breves 2—5 (*eb* 2—5)

2. Volar aspect of forearm and hand.

Palmar fascia (*fp*)

Palmaris superficialis (*ps*)

Palmaris profundus (*pp*)

Ulnaricarpalis (*uc*)

Flexor ulnaris (*fu*, *fu'*)

Flexor radialis (*fr*)

Pronator (*p*)

Flexores breves superficiales (*fbs*)

Flexores breves profundi (*fbp*)

Flexor interphalangeus digiti quarti (*fi*)

Carpometacarpales (*b*, *cd*, *ef*, *gh*, of the four digits respectively)

Intermetacarpales (*im* 1—3)

D. Muscles of the pelvic girdle and the proximal portion of the free limb.

1. Ventral aspect of the pelvic girdle.

Puboischiotibialis (*pit*)

Puboischiofemoralis externus (*pife*)

Pubotibialis (*pt*)

Ischiofemoralis (*isf*)

2. Caudal muscles attached to the posterior appendicular skeleton.

Ischiocaudalis (*isc*)

Caudalifemoralis (*cf*)

Caudalipuboischiotibialis (*cpit*)



3. Dorsal aspect of pelvic girdle.  
     Puboischiofemoralis internus (*pifi*)
4. Lateral aspect of girdle and limb.  
     Iliotibialis (*it*)  
     Ilioextensorius (*ie*)  
     Iliofibularis (*if*)  
     Femorofibularis (*ff*)

E. Muscles of the distal portion of the posterior limb.

1. Dorsal aspect of the leg and foot.  
     Femorometatarsalis (*fm*, *fm'*)  
     Extensor tibialis (*et*)  
     Supinator (*s*)  
     Extensor fibularis (*efb*)  
     Extensores breves 2—5 (*eb* 2—5)
2. Volar aspect of leg and foot.  
     Plantar fascia (*fp*)  
     Plantaris superficialis (*ps*)  
     Plantaris profundus (*pp*)  
     Fibularitarsalis (*fbt*)  
     Flexor fibularis (*ffb rud. 1., rud. 2.*)  
     Flexor tibialis (*fft*)  
     Pronator (*p*)  
     Flexores breves superficiales (*fbs*)  
     Flexores breves profundi (*fbp*)  
     Flexor interphalangeus digiti quarti (*fi*)  
     Tarsometatarsales (*b, cd, ef, gh*, of the four digits  
         respectively)  
     Intermetatarsales (*im* 1—3)  
     Interosseus (*io*)

In the selection of the abbreviations, which here follow the names of the muscles and are used in lettering the figures, while they are, in general, those suitable to the anatomical names, an attempt has been made, where possible, to employ the same letters for corresponding muscles in the two limbs. Thus, in such cases as Pronator, Flexores breves superficiales, etc., both name and abbreviation are the same in both, while in cases like the two Palmares, as compared with the Plantares, the names are sufficiently similar to allow the use of identical abbreviations. Far from causing a confusion thereby, it is intended to simplify matters,

and suggests some of the conveniences which would result from a more complete correspondence in the nomenclature of the two limbs.

The description of the separate muscles follows:

## A. Muscles between the trunk (or head) and the shoulder-girdle.

### 1. Dorso-lateral aspect.

*M. latissimus dorsi (ld)*. This muscle, the most posterior of the group, is in the form of a broad fan-shaped sheet, covering the sides of the body between the fifth and the eighth myocommata, and completely concealing *M. serratus anterior*, which lies beneath it. The more anterior fibers, about one half of the muscle, take their origin in a very thin, perfectly transparent aponeurosis, which lines the under side of the skin in that region, so that the fibers seem to be attached to the skin directly. The remaining half is in its origin divisible into two slips, which arise from myocommata 7 and 8 respectively. The slip from myocomma 8 runs almost horizontally forward and its fibers are the most posterior of the sheet; those of the slip from myocomma 7 run more obliquely and the most anterior of these are directly continuous with the most posterior fibers of the anterior half.

From this extensive origin the fibers converge to the glenoid fossa, where they become inserted along the proximal side of a stout tendon common to it and to *M. anconeus scapularis*. This tendon, which furnishes insertion for the latissimus but origin for the anconeus, is attached to the antero-lateral lip of the glenoid fossa, and serves to reinforce the capsular ligament of the shoulder joint.

*M. dorsalis scapulae (ds)*. This is a narrow, fan-shaped muscle, which covers the lateral (outer) surface of the scapula and suprascapula. It thus belongs in the same series with the procoracohumeralis and supracoracoideus, which together cover the three divisions of the shoulder-girdle. However, instead of arising from a large part of the area which it covers, as is the case with the two just named, the dorsalis scapulae arises from a narrow, curved line upon the suprascapula, parallel with the free margin and quite near to it; throughout the remainder of its course it is free from the skeletal part which it covers. It converges to its insertion into

the outer (lateral) surface of the cartilaginous proximal epiphysis of the humerus.

*M. omohyoideus* (*oh*). With some hesitancy this name may be given to a narrow slip which extends obliquely from the region back of the external gills to the notch between the scapula and the procoracoid, crossing in its course the dorsolaryngeus, and adjacent at its insertion to that of the trapezius, with which it there becomes parallel. It arises from the third epibranchial, or from the connective tissue in its vicinity, and extends obliquely from an antero-dorsal to a postero-ventral position. It inserts into the anterior margin of the shoulder-girdle in the deep notch between the scapula and procoracoid, adjacent to the insertion of the trapezius.

*M. trapezius* (*t*). This muscle is a thin sheet, which tapers down from a broad origin to a narrow band, and continues thus in the direction of the most posterior fibers. Like the latissimus dorsi its fibers arise from a transparent aponeurosis, which is closely applied to the under side of the skin, so that the fibers appear to rise directly from this latter surface. The origin is in great part covered by the *Mm. levatores arcuum* and dorsolaryngeus, which need to be dissected free and turned down in order to expose it. Unlike the corresponding muscle of the higher Urodeles, no fibers arise from any portion of the head, but the entire origin, in the relationship above described, extends between the second and fourth myocommata, and covers laterally the dorsal trunk muscles. The trapezius is inserted into the anterior margin of the osseous scapula along nearly its entire length.

*M. levator anguli scapulae* (*ls*). This is a very narrow band of muscle, which extends horizontally from the skull to the suprascapula, and lies mainly in the interval between the dorsal mass of trunk muscles and the visceral system, but belongs with the former. It arises by an extremely fine tendon from the posterior edge of the exoccipital bone, lateral to the condyle, the tendon being somewhat expanded at its origin. This tendon extends for a distance about equal to the width of a myotome, where it becomes continued as a narrow fleshy slip, which runs posteriorly in the interval between the dorsal trunk muscles and the branchial arches; after emerging from which it is still covered by *Mm. levatores arcuum*, dorsolaryngeus, and trapezius. The insertion takes place by means of fleshy fibers into the anterior angle of the suprascapula, just within the margin and thus upon the medial (inner) surface, and closely

associated with the fibers of insertion of the most ventral slip of *M. serratus anterior*. The tendon of this muscle is extremely difficult to follow to its origin in the occipital bone, and is best seen in a specimen from which the entire floor of the mouth and pharynx, together with the gill arches, has been cut away. The muscle may then be found at its scapular end and followed forward.

*M. serratus anterior (sa)*. This muscle is entirely covered externally by the *latissimus dorsi*, and consists of a series of flat slips (serrations) which arise posteriorly from myocommata, or from the distal ends of the ribs developed in them, and insert anteriorly into the medial (inner) surface of the suprascapula. There are three of these slips, the most ventral one from myocomma 7, the middle one from myocomma 6, and the most dorsal one from myocomma 5. The two anterior of these arise from the cartilaginous tips of the myocommatous ribs; the posterior from the myocomma itself. They insert into the medial surface of the suprascapula in an order corresponding to their origins, the one from myocomma 7 being the most posterior and so on. The most anterior of these slips becomes associated at its insertion with that of the *levator anguli scapulae*.

## 2. Ventral aspect.

*M. pectoralis (p)*. This muscle in *Necturus* is in the form of a single large sheet, not divided into separate slips or portions as in higher forms. It covers the entire pectoral region between the fifth and ninth myocommata. Its anterior edge is coincident with the middle fibers of *M. supracoracoideus*, which it overlaps; and as the fibers of the two have the same general direction at this place, and the pectoralis is very thin here, the two are easily taken for parts of a continuous sheet.

The origin of the pectoralis is a very extensive one and includes the ventral portion of the ninth myocomma as well as the entire linea alba from the point at which the ninth myocomma meets it as far forward as the point described above, that is, to about the level of myocomma 5. Although this line of origin consists of two parts which meet each other at nearly right angles, the fibers form an uninterrupted series, thus making a continuous sheet of converging fibers. In direction the fibers composing this sheet differ from one another by a little more than 90°; the most lateral of these arising from the myocomma are nearly longitudinal, those crossing the mid-coracoid region are transverse and form a right angle with



the linea alba while those of the extreme anterior margin are inclined slightly downwards as they pass out to the insertion. The lateral myocommatous fibers are reinforced from beneath (on the dorsal side of the sheet) by small slips from myocommata 7 and 8, but these reinforcements are not seen when the muscle is viewed from its ventral aspect and become visible only by freeing the sheet from its underlying connective tissue and reflecting it.

From the above extensive origin the fibers converge to a restricted fleshy insertion into the crista lateralis of the humerus, at its apex and slightly upon the medial side.

### **B. Muscles between the shoulder girdle and the free limb.**

*M. supracoracoideus* (*sc*). This muscle and the next, together with *M. dorsalis scapulae*, are the three muscles that cover the outer surfaces of the three subdivisions of the shoulder girdle, arising from these surfaces and inserting into the proximal epiphysis of the humerus. This muscle is incompletely divisible into two portions, of which the larger, or main, portion arises by a fleshy origin covering the middle third of the outer surface of the cartilaginous coracoid, and leaving free from muscular attachment a portion about the free anterior margin, as well as the basal third, that is, the part lying nearest the glenoid fossa. The second portion of the muscle is continuous with the first along its antero-lateral aspect and arises from the margin of the deep sinus between coracoid and procoracoid, running up somewhat upon the base of the latter. The two parts are blended along their entire extent, and insert as a single muscle into the crista lateralis of the humerus, just proximal to the insertion of the pectoralis.

*M. procoracohumeralis* (*ph*). This is the third and last of the muscles that cover the outer surface of the separate elements of the shoulder girdle. It lies upon and nearly covers the ventral aspect of the procoracoid, leaving exposed only the free anterior end of the cartilage. The surface of origin includes approximately the anterior half of this piece, extending laterally and medially from edge to edge. The distal half of this muscle, that lying towards its insertion, is not attached to the cartilage and is separated from it by the two slips of the rectus superficialis hypobranchialis posterior, which differentiate from the trunk musculature upon either side of the cartilage and run over its free edges to insert into its



outer surface. A semi-detached slip, apparently belonging to the procoracohumeralis, lies in the form of a narrow ribbon along its dorsal border, at first between it and the lateral slip of the superficial rectus and then between it and the dorsal portion of the supracoracoideus. Its origin is beneath the rest and nearer the glenoid fossa; its insertion appears quite separate and associated rather with the accessory portion of the dorsalis scapulae than with the procoracohumeral.

*M. rectus superficialis hypobranchialis posterior (rhp)*. Three more or less separate elements belonging to this system of trunk muscles become differentiated from the general mass and are inserted upon the external surface of the shoulder girdle. They consist primarily of a medial and a lateral portion, which embrace the procoracoid between them as they pass to their insertion, but the lateral slip is again capable of division into two because of a double origin. The details of these slips are as follows:

a) medial slip. This slip arises in the form of a thin sheet from the third myocomma, the origin including the lateral half of the distance between the procoracoid cartilage and the mid-ventral line. From this origin the fibers converge to a narrow insertion upon the external surface of the shoulder girdle, just anterior to the glenoid fossa, and thus on neutral ground between the shoulder pieces although at the base of the procoracoid.

b) lateral slip. This portion is double at its origin and consists of two heads, medial and lateral, although both soon unite and pass around the lateral side of the procoracoid as a single slip. The medial head arises from the third myocomma as a continuation laterally of the medial lateral slip (a), but passing laterally soon joins the lateral slip (b). Thus this head and the entire slip (a) represent a continuous superficial sheet that arises from myocomma 3 and is parted into two unequal portions by the procoracoid cartilage. The lateral head is much the larger, and arises from the posterior aspect of the first ceratobranchial cartilage and runs posteriorly, picking up on the way the small medial head. The combined bundle passes around the lateral margin of the procoracoid, and inserts upon the dorsal margin of this cartilage, in the region of and including the slightly projecting angle found there. The lateral head, which arises from the hyobranchial skeleton, is called by DRÜNER, *M. procoracohyoideus* (better *M. hyoprocoraccideus*); the medial head is plainly a semi-detached portion of the medial slip (a).

The homologising of this muscle, which with some variation is a fairly constant one in urodeles, has caused much trouble. HOFFMANN, in his careful summary of amphibian muscles, names the ventral mass of myotomic muscles lying between the sternal rudiments and the hyobranchial apparatus the "thoracicohyoideus" and treats these slips as auxiliary fibers, in which he and others are inclined to see the equivalent of the omohyoideus. DRÜNER does not find a separate omohyoideus, or, as he prefers to call it, a "pectori-scapularis", in either *Necturus* or *Proteus*, but thinks that in spite of the difference of insertion, the omohyoid elements may be found somewhere in these slips. Although in his description of this muscle in *Necturus* he says of the two slips arising from myocomma 3 that "ihr Ansatz unterscheidet sich so sehr wesentlich von dem des M. omohyoideus" (p. 606) under *Proteus* he wishes to see some connection between the two. "Da ein M. omohyoideus (pectori-scapularis) bei *Proteus* fehlt, liegt der Gedanke nahe, diese Muskeln, deren Verlauf und Habitus eine gewisse Ähnlichkeit mit jenem nicht verkennen läßt, mit ihm in Verbindung zu bringen" (p. 591).

*M. anconeus* (= triceps). This muscle occupies the entire dorsal or extensor surface of the humerus and is the homolog of the muscle found in the same locality in all tetrapod vertebrates, and usually called the "triceps" from the name given to it in Man, where it normally has three heads. In all cases the muscle arises from several points of origin, and is thus composed of several slips, which unite distally to form a stout tendon that inserts into the olecranon process of the ulna.

In *Necturus* there are four heads, as follows:

- anconeus scapularis* (as),
- anconeus humeralis lateralis* (ahl),
- anconeus humeralis medialis* (ahm),
- anconeus coracoideus* (ac).

Of these the two first are visible superficially from the lateral aspect, the first and the fourth from the medial aspect, while the third, which is the largest and deepest, is covered by the others. They may now be taken up in order:

*anconeus scapularis* (as). This muscle forms the dorsal (extensor) contour of the upper arm. It is a large muscle, the proximal half forming a rounded belly, while the distal half becomes flattened towards the olecranon. It arises from the antero-lateral lip of the glenoid fossa by means of a broad, firm ligament, that serves as a portion of the capsular ligament of the shoulder joint. The latissimus dorsi inserts by a tendon into the same ligament, and thus the origin of the former and the insertion of the

latter are somewhat confusedly blended. Indeed, it may be almost better to ascribe to the latissimus the tendon that inserts into the lip of the glenoid fossa, and consider that the fibers of the anconeus scapularis take their origin from the distal edge of this tendon. Viewed from the inner aspect, however, the two muscles appear to hold the common tendon between them, the fibers on the one side being those of the insertion of the latissimus, the fibers upon the other those of origin for the scapular anconeus.

The point of attachment of this common tendon is a very definite one, namely, into the antero-dorsal lip of the glenoid fossa, including both a projecting portion and a slight notch behind it, where the lip of the fossa is almost deficient.

*anconeus humeralis lateralis (ahl)*. This portion, the smallest of the four slips that make up the muscle, is a thin band of parallel fibers lying obliquely across the lateral (outer) side of the upper arm. It arises from the outer side of the shaft of the humerus at its proximal edge, almost at the boundary between the bone and cartilage. It is closely associated with the *anconeus humeralis medialis*, from which it is separated by the large vessels which pass between the two.

*anconeus humeralis medialis (ahm)*. This portion, which may be distinguished as the *profundus*, is the deepest, and perhaps the largest, of the four slips. It arises by fleshy fibers from almost the entire dorsal face of the shaft of the humerus, covered by the two preceding portions.

*anconeus coracoidens (ac)*. This is a medium sized band, obliquely placed, and extended across the medial aspect of the humerus, dorsal to *M. coracobrachialis longus* and nearly covering *M. scapulohumeralis*. It arises from the posterior tuberosity of the coracoid, just posterior to the glenoid fossa, runs as a distinct slip as far as the distal third of the humerus, where it blends with the inner edge of the *anconeus scapularis*.

The four heads above described unite to form a very stout tendon, which is of about the same caliber as the projecting olecranon process of the ulna, to which it is attached, and thus may almost be said to become continuous with it rather than to be inserted into it.

*M. coracobrachialis longus (cbl)*. This muscle and the *humeroantibrachialis inferior* are the two long muscles of the flexor surface of the upper arm, the former lying upon the medial (inner),

the latter upon the lateral (outer) aspect. The two thus correspond in general position to *Mm. biceps brachii* and *brachialis anterior* of higher animals, and may be homologous with these, wholly or in part.

The *coracobrachialis longus* arises from the posterior tuberosity of the coracoid, medial to and in contact with *M. anconeus coracoideus*, but the two are wholly distinct. Proximally it is also in contact with *M. coracobrachialis brevis*, the origins of the two muscles being along the same margin and close to one another. The muscle inserts into the distal half of the shaft of the humerus, above the internal condyle.

*M. coracobrachialis brevis (cbb)*. This is a very deep muscle, almost entirely covered by others. It lies between the *supracoracoideus* on the lateral, and the *coracobrachialis longus* on the medial, side. It is in the form of a small triangular sheet, and covers an area that includes about the proximal third of the humerus. It arises, in contact with the foregoing muscle, from the posterior margin and tuberosity of the coracoid, the two lines of origin being parallel though not coincident. From this origin the fibers converge to their insertion along the medial aspect of the proximal third of the shaft of the humerus.

*M. scapulohumeralis (sh)*. This is a band-like muscle, passing obliquely from the posterior margin of the scapular region, between *Mm. anconeus coracoideus* and *anconeus scapularis*, to the humerus. It arises from the margin of the deep sinus between the scapula and the tuberosity of the coracoid, and includes a small portion of the osseous scapula as well as the adjacent cartilage. It inserts along a line which runs lengthwise along the medial side of the shaft of the humerus and includes approximately the middle third of the osseous shaft of that bone.

*M. humeroantibrachialis (ha)*. <sup>Biceps</sup> This muscle lies along the flexor side of the upper arm and, while seen superficially from the lateral aspect, is equally well seen from the medial after the removal of the two *coracobrachiales*; in fact, the origin and insertion are better shown from the latter aspect. It arises from the *crista lateralis* of the humerus along its distal aspect, and extends along the entire shaft of the humerus. Crossing the angle of the elbow this muscle enters the antibrachial region on the radial edge between the flexor and extensor masses, and inserts by a flattened tendon into the lateral (radial) edge of the radius at the point



where the epiphysis joins the shaft, including in its field of attachment both cartilage and bone.

### C. Muscles of the distal portion.

#### 1. Dorsal aspect of forearm and hand.

*M. humerometacarpalis* (*hm*). This is the large superficial muscle, triangular in shape, that covers the central part of the dorsal surface, between *Mm. extensor radialis superficialis* and *extensor ulnaris*. It arises from the lateral condyle of the humerus and diverges fan-like to about the level of the distal row of carpal bones, where it becomes divided into three main slips, corresponding to the intervals between the digits. Closely associated with the outer one of the three main slips there is situated an accessory slip, which continues the series upon the ulnar side. It arises by a tendon of its own that lies upon the ulnar side of the main muscle in the form of a fine thread, and gives rise, not only to the fibers that form the accessory slip, but also to a few of the most ulnar fibers of the main bundle adjacent to it. The tendon lies closely approximated to that of the ulnar extensor, and in some cases it seems as though there was a direct connection between the two muscles.

Arrived at the interdigital spaces each of the three main slips divides distally into two, which insert by small tendons into the lateral angles at the bases of two adjacent metacarpals. Thus the two tendons of the most radial slip supply the ulnar side of digit II and the radial side of digit III; those of the second the ulnar side of III and the radial side of IV; and those of the third the ulnar side of IV and the radial side of V. The accessory slip passes to the outer (ulnar) side of the origin of *M. extensor brevis* V and inserts into the outer (ulnar) side of the base of metacarpale V.<sup>1)</sup> It thus

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1) In the foot this accessory slip seems to have been noticed by several observers, but its presence in the hand also has been overlooked, although, in *Necturus* at least, the two members are exactly alike in this respect. Thus HUMPHREY, describing the foot of *Cryptobranchus*, calls it "*M. peroneus tertius*", and HOFFMANN describes it as a general Urodelan muscle under the name of "*M. femoro-tarsali-fibulare*", but considers it a part of the "*Femoro-digiti I—V*" (= my femorometatarsalis). OSAWA mentions the statements of both HUMPHREY and HOFFMANN, but



completes on the ulnar side of the last metacarpal the series of tendons that supply the lateral aspect of the bases of the metacarpals, and serve as abductors and adductors of the set. The radial side of digit II alone remains unsupplied from this muscle, but the lack is supplied by a special abductor, *M. supinator*, which thus renders the series complete.

Judging by the accounts of this muscle in various Urodeles, as given by different authors, it seems certain that it changes its insertion relationships within the Order in question, beginning in the lower forms as a set of ad- and abductors and becoming ultimately, in the higher ones, in association with the extensores breves and their tendons, almost like the extensor digitorum communis of higher animals. Indeed, this final relationship is so nearly attained in some cases that many writers designate it as such even while describing it as more an ad- and abductor and less an extensor. In this gradual evolution *Necturus* takes the lowest place and the true condition of this muscle has been already pointed out by HUMPHREY, 1872, who compares it to the condition found in Saurians and in the *Ai*, and by ST. JOHN BROOKS, 1889, who describes it in some detail. Neither of these authors, however, speak of the separation of the interdigital bundles into two, nor, consequently, of the ultimate insertion of the tendons.

The next phylogenetic stage seems to be represented in *Cryptobranchus*, in which the muscle is already in effect an extensor. HUMPHREY, 1872, calls it *M. extensor digitorum sublimis*, and says that "passing down the forearm and over the carpus, and receiving upon its under surface fibres from the extensor digitorum brevis, it divides to the four digits, passing to the terminal phalanges". OSAWA, 1902, describes it under the name of *M. extensor digitorum longus*, and says that it "zieht direkt abwärts zur Handwurzel und teilt sich an der Basis der Metacarpale II—V in 4 sehnige Zipfel, welche in die Dorsalaponeurose der betreffenden Finger übergehen. Die letztere setzt sich ihrerseits aus der Sehne des vorliegenden Muskels und der später zu erwähnenden Muskeln, wie Abductor digiti secundi, Extensor digiti quinti proprius und Extensor digitorum brevis zusammen und geht distalwärts zur Endphalange der Finger, wo sie ihren Ansatz findet". He thus modifies the statement of HUMPHREY a little, in making the digital tendons of the separate digits less definitely portions of the muscle, but rather the somewhat differentiated median portions of a dorsal aponeurosis common to several muscles, thus forming an interesting early stage in the evolution of a definitive extensor of the fingers. These two authors, HUMPHREY and OSAWA, used in their study the large Japanese species, but EISLER, 1895, presents a similar picture of the condition in the allied *Cryptobranchus allegheniensis*, in which the muscle

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does not consider the slip in question to be worthy of the rank of a distinct muscle. In the hand he finds nothing to correspond to it, but in *Cryptobranchus*, his subject of study, the part may indeed be wanting.

mass terminates at the base of the metacarpals in a "Sehnenwulst", from which four flat tendons run to the four fingers, "außerdem aber kurze Faserzüge sich seitlich auf die Basis der Metakarpalien, auch der marginalen, heften". These "Faserzüge", which prolong the tendons laterally, convert the latter into the "Dorsalaponeurose" of OSAWA, although EISLER says nothing of the participation of other muscles in its formation.

RIBBING, 1906, perhaps the most recent writer on the subject, describes in the Axolotl (*Siredon*) an interesting condition in the "langer Streckmuskel" of the arm, which may serve as a link between the condition in *Necturus*, where the muscle stops at the bases of the metacarpals, and that of *Cryptobranchus*, where the partly differentiated tendons of the dorsal aponeurosis form its extension to the terminal digits, for here the muscle, which involves only digits III—V, "inseriert mittels kurzer Sehnenzipfel an den Bases der Metacarpalia III—V und hat auch schwache Verbindungen mit den kurzen Extensoren der 3 ulnaren Finger [die kräftigste dieser Verbindungen ist die mit den kurzen Extensoren (dem kurzen Extensor?) des 5. Fingers]". This condition, which incorporates the short extensors and their tendons with the humerometacarpalis, may be easily derived from that in *Necturus*, through a closer attachment between the terminal lips of the latter and the origins of the former, a condition almost realised in the corresponding muscle of the *Necturus* foot, where the connection between the two muscles is very close.

The next logical step would seem to be the complete suppression of the extensores breves as independent muscles, and the employment of their tendons by the compound muscle while the lateral tendons to the bases of the metacarpals are still retained. This stage corresponds exactly to EISLER's description of the condition in *Salamandra*, where the muscle splits in the carpal region into three bundles "die je eine lange Sehne für die Endphalangen der drei ulnaren Finger bilden, daneben aber noch jederseits (an Dig. V. nur radial) Sehnenzipfel zu den zugehörigen Metacarpalbasen schicken".

Although the idea of a gradual differentiation in this muscle within the group of urodeles seems to be expressed in the writings of recent investigators, such does not seem to have been the thought of the earlier writers, who seem to have taken it for granted that a typical extensor would be found in all cases. Thus HOFFMANN, 1878, although he had before him the work of HUMPHREY, describes this muscle, under the name of *M. humero-digiti II—V*, as dividing "in vier Sehnen für die vier Finger, an deren Endphalanx sie sich inserieren". As examples of this condition he gives *Menobranchus*, *Cryptobranchus*, *Siredon* and *Salamandra*.

The corresponding muscle of the foot, *M. femoro-metatarsalis*, is like the humero-metatarsalis and its gradual evolution through the Order of Urodela seem also to be the same.

*M. extensor radialis (er)*. This is the very large mass of muscles which lies on the radial side of the forearm, partly covered by the humero-metacarpalis. After the removal of the latter it is seen to almost entirely cover the dorsal surface of the radius and

to extend at its proximal end so that it comes in contact with the extensor ulnaris. It is divided into two portions, with origins in contact but with distinct insertions. A large nerve (*R. dorsalis manus intermedius* of OSAWA?) passes between the two portions. The details are as follows:

a) *Extensor radialis superficialis (ers)*. This portion arises from along a longitudinal line upon the lateral condyle of the humerus, higher up than any other muscle of the group; the lower end is in contact with the origin of the humero-metacarpalis. Almost as soon as the radius is reached the deepest fibers of this portion begin to insert along its free margin, and continue down the entire length of the bone. The remaining fibers pass under the margin of *M. supinator*, and insert in two bundles, into the marginal and dorsal aspects of *radiale* and *carpale II* respectively. The most superficial of the fibers of this muscle are the longest, and consist of those that insert into *carpale II*; beneath these lie the fibers that insert into the *radiale*, and the deepest of all are those that insert into the radius.

b) *Extensor radialis profundus (erp)*. This portion lies medial to the former and is wholly covered by the humero-metacarpalis. It arises from the lateral condyle of the humerus, along a transverse line just distal to and parallel with that of the latter muscle. This origin, tendinous at first, becomes muscular almost immediately and the fibers insert along the greater part of the ulnar margin and more than the ulnar half of the dorsal aspect of the radius, including in length the most of its shaft.

*M. supinator (s)*. This muscle is easily distinguished since it is the only one on the dorsal aspect of the limb that is obliquely placed. The terminal portion alone is superficial and may be seen emerging from beneath the humero-metacarpal upon the radial side; the remainder is concealed by this latter muscle, which must be removed in order to expose it. It is a shorter muscle than its homolog in the leg, and lacks entirely an origin from the ulna (corresponding to that from the tibia), but its two other origins from the carpal bones correspond exactly to those from the tarsus. The muscle thus arises by superficial fibers from the radial margin and a bit of the dorsal surface of the ulnare-intermedium, and by a deeper slip from the centrale, these latter being best exposed by cutting through the muscle near its insertion and reflecting it. The muscle is inserted by a tendon into the radial margin of meta-

carpale II, near the base of the bone, and thus acts as an abductor of the digit, completing the system formed by the tendons of insertion of the humero-metacarpalis and its accessory slip.

*M. extensor ulnaris (eu)*. This muscle occupies the outer (ulnar) margin of the leg and is partly overlapped by the humero-metacarpalis. It arises from the lateral condyle of the humerus, along the margin adjacent to the olecranon process of the ulna, and runs down over the dorsal surface of this latter bone, covering it completely. The more superficial and marginal fibers are the longest, and enwrap and conceal the others in such a way that the muscle needs to be drawn away from the limb a little and unrolled, as it were, in order to appreciate its method of insertion; this has been done in the figure (Fig. 22) and shows the termination of the area of insertion along an oblique line on the lower part of the ulna and on the margin of the ulnare-intermedium. Above this line the remaining fibers insert, covered by the more superficial ones, so that the total area of insertion includes the entire length of the shaft of the ulna along its marginal border, extending, at about the middle of the shaft nearly or quite across the bone. Aside from this extensive insertion on the ulna a few of the outer fibers become inserted into the marginal aspect of the ulnare-intermedium, beyond which the fascia continues over the edge of the paw and invests the short finger muscles upon the flexor side.

*Mm. extensores breves (eb 2—5)*. These small muscles are four in number, one for each digit, and appear superficially as oval bellies, interdigitating with the slips of the humerometacarpalis. They arise from the distal margins of the carpalia that correspond to the digits to which they belong, carpale 4 + 5 giving rise to two, as would be expected. The bellies are continued into long, narrow tendons, but partially differentiated from the aponeurosis that covers the dorsal surface of the digits, and appear as thickened stripes along the middle of the fingers. These nascent tendons insert into the bases of the terminal phalanges.

As stated in detail under *M. humerometacarpalis*, these short extensor tendons appear in higher urodeles as the proper tendons of this latter muscle, converting it into an extensor digitorum communis (*s. sublimis*). The steps of this change are very gradual and are well seen within the limits of the Order, the changes being due to modifications in the relationships of the two muscles in question. Thus in *Cryptobranchus*, in which these tendons are ascribed to the humerometacarpalis (forming an extensor digitorum longus) the lateral tendons to the bases of the meta-



carpals are also preserved, and the bellies of the extensores breves are described as accessory slips inserting into the under (ventral) surface of the long tendons (HUMPHREY, OSAWA). EISLER makes the short extensors much more complicated, dividing them into three layers with different conditions in the different regions, but OSAWA, who is not only the latest writer on the subject, but who had the advantage of studying the large *C. japonicus* in place of the much smaller *C. allegheniense*, which was the one used by EISLER, finds nothing of this, and describes them as simple muscle bellies, with the relations as described above for *Necturus*.

## 2. Volar aspect of forearm and hand.

Palmar fascia (*fp*). The muscles of the volar surface of the forearm and hand are covered superficially by a fascia which, distal to about the middle of the forearm, becomes thick and opaque, concealing all subjacent parts. This latter portion is the palmar fascia proper, and extends distally as a continuous sheet from the distal margin of *M. palmaris superficialis*, of which it forms an aponeurotic continuation. At about the base of the metacarpals it divides into four slips, which gradually narrow and lie along the volar aspects of the four digits, inserting into the bases of the terminal phalanges. These tendon-like strips are tied down by ligaments opposite the metacarpo-phalangeal joints, and, in the case of digit IV, opposite also the extra joint between phalanges 1 and 2. While opposite the row of carpalia, and shortly before its division into the four digital slips, the palmar fascia becomes firmly fastened to the distal border of these bones, and the crescentic partition of firm connective tissue thus formed, and the surface of the fascia adjacent to it distally, furnish the points of origin for the two sets of short flexors of the digits. Proximal to this partition the *palmaris profundus* becomes inserted into the dorsal (inner) surface of the fascia. The entire set of muscles thus united into a system through the medium of the palmar fascia includes both superficial and deep palmar muscles, as well as the two sets of short flexors, *superficiales* and *profundi*, and the whole acts as a compound flexor of the digits.

Certain authors, including recent ones (OSAWA), have considered the digital portions of the fascia to be the tendons of a long flexor, the *palmaris superficialis* being the muscular belly associated with it. That the definite long flexor system of higher animals becomes derived from a condition similar to that in *Necturus*, and that we have here such a system almost begun, cannot be doubted, but in view of the complex relationship of the fascia to many muscles it seems best to treat it as has here been



done, that is, as a fascia that furnishes attachment to many muscles without being a definite part of any of them. (See also the remarks below, sub plantar fascia.)

*M. palmaris superficialis (ps)*. This is a short, broad muscle occupying the proximal half of the antebrachium, and is continued directly into the palmar fascia. It arises by fleshy fibers from the medial condyle of the humerus, between the similar origins of the radial and ulnar flexors. From their origin the fibers diverge and form a broad belly, which inserts, when at its greatest breadth, into the proximal margin of the palmar fascia.

According to McMURRICH this insertion is in reality between the two layers which compose the fascia, these latter investing the muscle upon both sides and forming the fascia by their union.

*M. palmaris profundus (pp)*. This muscle arises in two parts, separated almost completely by a narrow bundle of longitudinal fibers, the ulnaricarpalis, a specially differentiated portion of the same system. Both parts arise in the main along narrow lines that run parallel to each other upon the radio-flexor aspect of the shaft of the ulna, and continue across the surface of the ulnare-intermedium; in addition to this some of the distal fibers of the more ulnar portion arise from the side of the tendon of the ulnar flexor, and still other fibers arise from the surface of carpale 4 + 5 and connect the two portions of the muscle. The muscle inserts as two adjacent bundles into the dorsal (inner) surface of the palmar fascia, covering a large area.

*M. ulnaricarpalis (uc)*. This muscle consists of a long narrow band, running lengthwise through the mass of flexor muscles of the forearm. It arises along a line placed longitudinally upon the shaft of the ulna, on the margin turned towards the radius, and occupying its proximal half. It thus lies between the lines of origin of *Mm. pronator* and *palmaris profundus*, and the muscle itself rests upon the former and parts the fibers of the latter into two bundles on its way to its insertion. This latter occupies a small area in the very middle of carpale 4 + 5, just proximal to the line of origins of the *Mm. carpo-metacarpalia*.

*M. flexor ulnaris (fu, fu')*. A large muscle, lying upon the flexor surface of the ulna, and forming the ulnar contour of the flexor side of the antebrachium. At its origin it consists of two parts, which arise in contact with one another from the ulnar aspect of the median condyle of the humerus. The more proximal of these

two portions (*fu'*) is very short; its fibers run obliquely outwards and wrap themselves about the olecranon, inserting into the side of this process and upon the shaft of the ulna beneath it.

The second or main portion (*fu*) is somewhat fusiform, and is longitudinal in direction. It lies along the outer edge of the entire shaft of the ulna and tapers down into a terete tendon, which terminates on the outer, or marginal, aspect of carpale 4 + 5, but seems to be also prolonged along the margin of the carpus, to a further insertion into the ulnare-intermedium.

*M. flexor radialis (fr)*. This muscle forms, upon the other side of the antebrachium, the counterpart of the preceding; like the latter, it determines a part of the contour of the forearm, yet is a somewhat shorter muscle. It arises from the medial condyle of the humerus upon its radial side and inserts by fleshy fibers into a broad area which includes both the distal end of the radius and the radial half of the radiale.

*M. pronator (pr)*. The fibers of this broad muscle run obliquely across the antebrachium from a more proximal ulnar to a more distal radial position. It is thus directly coincident with the supinator of the other side; that is, if the paw were semi-transparent, and were held up to the light, the two muscles would be superimposed one upon the other. The pronator arises from the middle of the shaft of the ulna by a narrow line, running lengthwise and just within (radial to) the lines of origin of the ulnarcarpalis and the inner half of the palmaris profundus. It inserts by two slips, the one into the proximal side of carpale 2, the other into the radial side of the base of metacarpale II. Corresponding tho these two insertions the muscle is incompletely divided into two sheets, of which the deeper one is much the smaller, and makes its insertion into the carpale, while the bulk of the muscle inserts into the metacarpal, and forms an abductor of digit II in precisely the same way as does the supinator on the extensor side.

*Mm. flexores breves superficiales (fbs)*. These are a series of short fleshy bundles, covering the metacarpals of the separate digits; after the removal of the skin they are seen in part upon either side of the digital slips of the palmar fascia. They are capable of separation into distinct elements mainly through their insertions, so that the mass supplied to each digit is a bundle of more or less separate slips rather than a single muscle. They all arise from the dorsal (inner) surface of the palmar fascia, partly

from the crescentic ligament that binds the latter to the carpalia and partly from the fascia distal to this and proximal to the point at which it splits into the slips for the separate digits. The subdivisions and their insertions are not quite the same in all the digits, but the fundamental plan seems to be that of one median and two lateral slips, the lateral being once more subdivided. The median slip is the most distal in origin, and, consequently, the most superficial; it inserts into the base of the proximal phalanx (in the case of digit IV. into the base of the second phalanx). The lateral slips insert into the margin of the digit, one part into the distal end of the metacarpal, the other into the proximal end of the proximal phalanx. These two parts are separated by the metacarpo-phalangeal articulation. Allowing for some individual variation, the way in which this plan is carried out in the different digits is as follows:

Digit II: radial bundle equal in bulk to half that of the entire muscle; ulnar bundle very small.

Digit III: corresponds closely to the type.

Digit IV: a variation is here introduced because of the extra phalanx. The median bundle inserts into the base, not of the proximal, but of the middle phalanx, leaving the former to be supplied by the flexor brevis profundus only. The median bundle, in order to accomplish this, is supplied with a tendon of some length, while in the other digits this bundle, as in the case of the rest, makes a fleshy insertion.

Digit V: This is, in a way, the reverse of the condition in digit II, as here the ulnar, there the radial, bundle is the largest; in each case the marginal, or outer one with reference to the entire hand. The ulnar bundle is distinctly double, each part being well developed; the radial bundle is moderate.

Mm. flexores breves profundus (*fbp*). These consist of four small slips, barely in contact with one another at their origin and supplying the four digits. The system is entirely covered by the preceding, and thus constitutes a second layer of short muscles in the carpo-metacarpal region, in regard to its muscles the most complicated portion of the free limb. These muscles arise from the distal aspect of the crescentic ligament that holds down the palmar fascia, and the four slips are just broad enough at their bases to be in contact with one another at their corners. They may thus be considered as a single muscular sheet, divided into slips to its very base.

The slips are thin and ribbon-like and taper slightly distally. They are coincident with the entire extent of the metacarpals, and insert into the bases of the four proximal phalanges, the insertions being, in the case of digits II, III, and V, directly beneath the similar ones of the median slips of the flexores breves superficiales.

*M. flexor interphalangeus digiti quarti (f)*. This minute slips appears in the fourth digit alone, and is evidently an adaptation to the extra phalanx possessed by this digit, its purpose being the supply of the extra joint thus formed. It consists of a few muscle fibers stretched across the flexor aspect of the articulation between phalanges 1 and 2, and arises from the middle of the shaft of the former and inserts into the base of the latter. It is often divisible into two slips, placed side by side.

That this muscle is in origin an extension of the flexor brevis profundus of this digit is rendered extremely probable, not only by its appearance and general direction, but also by the occasional presence of one or more fibers that connect the two and form a part of both. Such a case, although not to be considered typical, has been selected as the one figured, the usual condition being shown in the case of the corresponding muscle of the hind limb (Figs. 34 and 35).

*Mm. carpometacarpales (b, cd, ef, gh; those of the four digits respectively).*

These form a third and still deeper layer of muscles between carpus and metacarpus, lying beneath both sets of short flexors. They are described by EISLER under the name of flexores breves profundi, those designated here by that name being called the medii; since, however, the carpo-metacarpales are not associated with the palmar aponeurosis, and since they are in their use adductors and abductors rather than flexors, they can hardly be treated as a part of the same system with the others.

They arise without exception from the distal margin of the carpalia and insert into the shafts of the several metacarpals by oblique lines of insertion. Typically there are two for each metacarpal, the one radial, the other ulnar, and as they are inserted lateral to the median line of the digits they move the metacarpals laterally and thus assist in spreading and approximating the digits, a motion which, in this animal, is far more emphasized by the differentiation of the muscles than are flexion and extension, so characteristic of the movements of higher animals.

The details of the carpometacarpales in the separate digits are as follows:



Digit II: This is the only digit not supplied with a pair of these muscles, as the radial one is here wanting. Its place is, however, supplied physiologically by the pronator, which is inserted mainly into the base of the metacarpal of this digit upon its radial side and thus acts as a strong abductor. The ulnar slip arises from the radial portion of the distal margin of carpale 3 and inserts normally into the shaft of the metacarpal at the point given above in the general sketch.

Digit III: Furnished with a pair of muscles closely corresponding to the type. The radial one arises from carpale 3, the ulnar one in part from this and in part from carpale 4 + 5 and from the interspace between them.

Digit IV: Furnished with a pair of muscles closely corresponding to the type. Both arise from carpale 4 + 5.

Digit V: The radial mass is very broad. It arises from the ulnar half of the margin of carpale 4 + 5 and inserts obliquely along a line that is nearly as long as the entire shaft of the bone, the radial fibers being the longest. The ulnar muscle is the most eccentric in the series. It arises from the outer side of the tendon of *M. flexor ulnaris* and inserts upon the ulnar border of the metacarpal, the area of insertion being much restricted.

*Mm. intermetacarpales (im 1-3)*. These small muscles are the deepest of the entire series and, so far as location goes, may be equally well ascribed to either the flexor or the extensor side, although from their use as ad- and abductors of the separate digits they are better treated in this place, following other short muscles that are similar in function. They are in the form of thin, somewhat triangular sheets, that occupy the interdigital spaces, and may thus become partly visible by strongly separating the digits, even before the removal of any of the muscles. They extend across between the metacarpal bones, and may be said to arise from the radial aspect of metacarpalia III-V, where they are the narrowest, and to expand fan-like to broader insertions upon the ulnar margins of metacarpalia II-IV.

#### D. Muscles of the pelvic girdle and the proximal portion of the free limb.

##### 1. Ventral aspect of pelvic girdle.

*M. puboischiotibialis (pit)*. This is the most superficial of the muscular layers covering the ventral aspect of the pelvic



girdle, and is confined in *Necturus* to the posterior half of the pubo-ischiadic plate, although in most urodeles it extends over the entire ventral surface, completely concealing the puboischiofemoralis externus, which is here exposed anteriorly. The muscle is in the form of a triangular sheet, and takes its origin from the median line of the pubo-ischiadic plate for a little more than the posterior third of its extent, the surface of origin being slightly augmented through the development of a low median ridge, the *crista muscularis*. From this origin the fibers converge to the knee and lower leg, in which region they become inserted.

The muscular sheet thus defined is marked by two peculiar features, a raphé and a tendon. The raphé begins at the posterior border, about midway between origin and insertion, and runs anteriorly, at right angles to the fibers, fully half-way through the muscle, presenting the appearance of a broad and rather deep scar. It serves as the point of insertion for *M. caudali-puboischiotibialis*, a band-like muscle which comes up from the tail in company with two other caudal muscles, and is inserted into the raphé at the posterior border of the puboischiotibialis, the fibers of the two muscles involved running almost at right angles to each other. Aside from this caudal muscle there is an accessory bundle of fibers, situated upon the deeper (dorsal) surface of the puboischiotibialis, blended with the main muscle at the origin and inserted into the deep surface of the raphé. This bundle evidently represents the *ischioflexorius* of other urodeles, although it is here not sufficiently distinct to be considered a separate muscle.

The second feature mentioned above, the tendon, marks the antero-lateral border of the muscle, and is complicated as well as variable in its relationships. When best developed it is quite broad, visible superficially, and serves to define the boundary between this muscle and *M. pubotibialis*. It usually forms the direct continuation of the fibers of about the anterior third of the muscle, that is, of those not affected by the raphé, but in addition to these it receives a variable number of fibers along both edges; those inserting on the postero-medial edge arise from the distal side of the raphé, and those on the antero-lateral edge are derived from the adjacent muscle, *M. pubotibialis*. These relations are subject to considerable individual variation, and the tendon itself may vary in size from that described above to a delicate thread, sunk between the fibers and not visible superficially. In some cases it may seem more like a thin septum,

separating the fibers of the two adjacent muscles, and offering an insertion to both. There is also much variation in the number of fibers which come to it from the pubotibialis, as in some cases nearly a third of the entire muscle is involved, while in others but a few fibers insert into it, and these near its distal end. In one case noted a small slip from *M. puboischiofemoralis externus* was inserted into the proximal end of the tendon, mingled with the fibers of the puboischiotibialis; this peculiarity was unilateral, the other side being normal. In all cases the tendon, having served as an insertion, both at its proximal end and along its sides, for a variable number of fibers from *M. puboischiotibialis* and one or two others, becomes inserted into the inner aspect of the tibia, near its proximal end.

The posterior portion of the puboischiotibialis has nothing to do with the above tendon, but is continued as a fleshy mass, wrapped partly around the leg, and reinforced by auxiliary fibers from the transverse raphé. This and the former make separate insertions; the original fibers inserting along the shaft of the tibia, distal to the insertion of the tendon, while the auxiliary fibers pass farther around the leg to the fibular side and insert into a thin fascia, which overlies the plantar fascia and blends in part with it.

*M. puboischiofemoralis externus (pife).* This muscle arises from along the entire median line of the ventral surface of the puboischiad plate, from which its fibers converge to their insertion in the femur in such a way that the muscle is practically coincident in outline with the plate itself. The muscles of the two sides, taken together, thus form a fairly thick sheet that covers the entire ventral aspect of the puboischium. Of this sheet a little more than the posterior third is covered by the preceding muscle, *M. puboischiotibialis*, the remainder is superficial. The muscle is readily divisible into a larger anterior and a smaller posterior portion, differing both in origin and the direction of their fibers; and the first of these may be further subdivided, though not very definitely, into three bundles; a) anterior superficial, b) posterior superficial, and c) anterior deep. Of these portions a) is the most anterior and arises from the median line of the plate for about its anterior half, inserting into the crista ventralis of the femur and the distal prolongation of this process. Portion b) is a narrow slip, arising from the median line in the ischiadic region and inserting into the crista ventralis proximal to the insertion of a),

and closely associated with that of c). Portion c) is perhaps a little the largest, slightly exceeding a). It arises from the median line along approximately its middle three-fifths, and is overlapped anteriorly by a). It inserts into the crista ventralis.

The more posterior of the two main portions arises from the muscular ridge (crista muscularis) which characterises the posterior half of the ventral surface of the puboischium, and occupies with its origin nearly the posterior third of this latter piece. Its fibers are directed forwards and outwards, and run beneath (dorsal to) the other portion, which must thus be reflected in order to expose the insertion. This latter is upon the shaft of the femur dorsal to the crista ventralis, and is hence more dorsal in position than that of the anterior portion.

*M. pubotibialis (pt)*. This is a narrow muscular band, which lies along the inner side of the leg. It arises by a tendon from the projecting angle upon the margin of the puboischium, immediately anterior to the acetabulum, a projection which seems to have not received a name as yet, and which may be called the pre-acetabular process. The fibers of this muscle form a narrow ribbon, which runs along the side of the femur, parallel to its shaft, and becomes inserted by a short tendon into the proximal third of the shaft of the tibia upon its lateral aspect. The most posterior fibers of this muscle are semi-distinct from the rest, and insert in variable numbers into the tendon of *M. puboischiotibialis*.

*M. ischiofemoralis (isf)*. This small muscle arises from the outer margin of the tuberosity of the ischium and lies in the same plane as the skeletal plate, being covered ventrally by both puboischiotibialis and the posterior portion of the puboischiofemoralis externus. The fibers of this muscle converge from their origin and form a tendon, which inserts into the crista lateralis of the head of the femur.

## 2. Caudal muscles attached to the posterior appendicular skeleton.

*M. ischiocaudalis (ic)*.

*M. caudalifemoralis (cf)*.

*M. caudalipuboischiotibialis (cpit)*.

These three closely associated, ribbon-like bands lie in a common sheath formed principally by the ventral mass of the trunk muscles with the aid of the cloaca, which forms the medial wall. Of the

three muscles the ischiocaudalis is the most medial, and is also the most distinct. It is clearly a differentiation from the most ventral fibers of the trunk-tail muscles, and arises from them in such a way that it is impossible to definitely distinguish its slips of origin from those of the undifferentiated myotomic masses. In this region, the ventro-caudal, a thin aponeurosis, attached to the haemal spines, separates the muscle masses of either side from the mid-ventral mass of caudal glands, and forms a groove for the lodgement of the latter. From the dorsal surface of this the fibers of the muscle in question take their origin, the haemal spines most directly involved being the first three or four. From this origin the band-like muscle runs along the side of the cloaca, and inserts into the outer angle (tuberosity) of the osseous ischium.<sup>1)</sup>

The two other caudal muscles, Mm. caudalifemoralis and caudalipuboischiotibialis, arise from a common origin and as a single bundle, becoming distinct from each other anteriorly, and forming two long bands, like the former. The origin is in the form of a flattened mass or sheet, extending antero-posteriorly, and arising from the sides of the haemapophyses of the first three vertebrae provided with such a process, usually the 22nd, 23rd, and 24th. As the haemapophyses in this region are long and so inclined that they almost overlap, they form upon either side a practically continuous line of origin. Proceeding anteriorly the two muscular slips become differentiated and diverge somewhat to their insertions, points indicated in each case by the name. M. caudalifemoralis inserts into the shaft of the femur just distal to the projecting crista lateralis; M. caudalipuboischiotibialis terminates in the raphe of the puboischiotibialis, at the posterior border of the muscle.

### 3. Dorsal aspect of pelvic girdle.

M. puboischiofemoralis internus (*pifi*). This large muscle lies upon the internal (dorsal) surface of the puboischium, over the

1) Physiologically considered, the origin and insertion of this, and perhaps also of the caudalipuboischiotibialis, should be reversed, as the point of least motion is found in both cases to be the pelvic girdle. In accordance, however, with the anatomical structure the end associated with the axial skeleton would form the natural point of origin and thus they are described here. This method has the distinct advantage of treating all three closely associated muscles alike, whereas otherwise the course of direction of one would be the reverse of that employed in the description of the other two.



margin of which it curves to its extensive insertion on the femur. In following this course the muscle becomes divided into two portions by the ilium, which projects dorsally between its fibers, but these portions become joined again upon the outer side of the ilium by a bundle of fibers which arise from the lateral aspect of the ilium itself, and the three become absolutely continuous long before the insertion is reached. The muscle is thus extremely difficult to demonstrate and needs for its complete exposition views from several different aspects, the most of which demand special dissection and the sacrifice of many of the adjacent structures. Thus the part which is visible upon the outer side of the leg when the latter is in its more usual position (Figs. 11, 12) is merely the distal portion, and the manner of its insertion can be realised only by elevating the femur of a specimen from which the ventral muscles have been cleared (Fig. 13).

To study this muscle to advantage it is necessary first to remove from the body the entire puboischiadic plate with the legs attached, cutting through the ilia, and then to cut away entirely the iliac muscles of one side, especially *Mm. iliotibialis*, *ilioextensorius*, and *iliofemerofibularis*. The femur should be extended laterally and the projecting ilium should be cut off to about the level of the muscle.

Viewing this preparation now from the dorsal side the muscle in question is revealed throughout nearly its entire extent, and appears as a vast sheet, stretched between the puboischium and the femur, its fibers flowing completely around the truncated ilium and reuniting upon the other side (Fig. 14). Although anatomically the muscle is not easily separated into distinct portions it is convenient for purposes of description to divide it into three heads, anterior, middle, and posterior. The anterior portion arises from along the median line of the dorsal surface of the puboischium, extending from the anterior end of the epipubic process to the puboischiadic fossa. At its origin the muscle is in the form of a thin lamella, but receives from beneath additional fibers from the anterior side of the ridge that bounds the puboischiadic fossa anteriorly, after which the muscle becomes thicker and blends with the other portions. The posterior portion arises from the side and bottom of the puboischiadic fossa, its most anterior fibers approaching so nearly to the most posterior ones of the anterior portion that the two are separated only by the ridge that bounds the fossa anteriorly. The lateral or external portion arises from the outer surface of the



ossified part of the ilium and from the cartilage about its base, and is consequently shorter than are the other two portions. Beyond the ilium all the parts blend into an inseparable mass, but the fibers open up again in such a way that the final insertion into the shaft of the femur is along two oblique lines that converge distally towards the tibial side. In Fig. 13 the more ventral of these insertions is shown by itself, but in Fig. 14 and 17 the remainder is also visible. Viewed from without, in a specimen in which the puboischiadic plate remains in situ, the muscle, after the removal of the iliac muscles as directed above, appears as in Fig. 15.

Although in *Necturus* the three parts are inseparably blended as here described, and form a single muscle, it is quite likely that the iliofemoralis, described as a separate muscle in certain urodeles (*Salamandra*, *Siredon*) is the homolog of the lateral portion, the part that arises from the outer side of ilium.

#### 4. Lateral aspect of girdle and limb.

*M. iliotibialis (it)*. This muscle appears on the outer aspect of the thigh as the most anterior of the iliac muscles, overlapping posteriorly *M. puboischiofemoralis internus*. It arises by a bundle of fibers from the base of the ilium, just within the lateral edge of the puboischiadic plate, over which it curves to attain the outer side of the leg. It inserts by a narrow tendon into the proximal epiphysis of the tibia on its outer (extensor) aspect. This muscle is here distinct from the next, but in certain other urodeles appears to be fused with it, since HOFFMANN treats the two names as synonymous.

*M. ilioextensorius (ie)*. This muscle is the next posterior to the last and runs parallel to it. It arises by a narrow tendon, in common with that of *M. iliofibularis*, from the base of the ilium at the anterior boundary between the outer and inner aspects. The tendon of origin runs for some distance along the posterior margin of the muscle, and gives rise to the fibers that constitute its belly along the greater part of its length. The belly, which is in the form of a flattened band, becomes continued, immediately below the knee, into a broad aponeurosis, which spreads out over the joint and, in the form of a fascia, invests the muscles of the lower leg. Upon the tibial side of this aponeurosis there arises a small but firm tendon, which in some individuals assumes a considerable size and may thus be considered the direct tendon of insertion of the muscle.

This tendon runs down over the dorsal aspect of the lower leg, between Mm. femorometatarsalis and extensor tibialis, and inserts into the distal epiphysis of the tibia (Fig. 25 *ie*).

*M. iliofibularis (if)*. This narrow, fusiform muscle, parallel to and immediately posterior to the last, lies somewhat over the posterior edge of the thigh so that it is best seen from the inner aspect. It arises by a narrow tendon, in common with that of *M. ilioextensorius*, from the base of the ilium, and inserts into the proximal epiphysis of the fibula along its outer (posterior) aspect. It is treated by HOFFMANN in connection with *M. femerofibularis*, the two being considered by him as the two heads of a bicipital muscle, *M. iliofemerofibularis*, an indirect homolog of the human *M. biceps femoris*. In *Necturus*, however, the two muscles are entirely distinct, and make separate insertion into the fibula (Fig. 37 *if* and *ff*).

*M. femerofibularis (ff)*. This is a narrow, ribbon-like muscle, extending diagonally across the posterior (ventral) aspect of the shaft of the femur. It arises near the insertion of Mm. caudalfemoris and ischiofemoralis, and extends obliquely across the femur towards the fibular side of the lower leg (Fig. 14). It makes a tendinous insertion into the middle of the shaft of the fibula upon its outer aspect.

## E. Muscles of the distal portion of the free limb.

### 1. Dorsal aspect of leg and foot.

*M. femerometatarsalis (fm)*. This is the large superficial muscle, triangular in shape, that covers the central part of the dorsal surface, between Mm. extensor tibialis superficialis and extensor fibularis. It arises from the middle of the outer surface of the distal epiphysis of the femur, between the two condyles, and diverges fan-like to about the level of the distal row of tarsal bones, where it becomes divided into three main slips, corresponding to the intervals between the digits. Closely associated with the outer one of the three main slips there is situated an accessory slip which continues the series upon the fibular side. It arises by a tendon of its own that lies upon the fibular side of the main muscle in the form of a fine thread, which gives rise, not only to the fibers that form the accessory slip, but also to a few of the most fibular fibers of the main bundle adjacent to it. The tendon lies closely approxi-

mated to that of the fibular extensor, and in some cases it seems as though there was a direct connection between the two muscles.

Arrived at the interdigital spaces each of the the three main slips divides distally into two, which insert by small tendons into the lateral angles at the bases of two adjacent metatarsals. Thus the two tendons of the most tibial slip supply the fibular side of digit II and the tibial side of digit III; those of the second the fibular side of III and the tibial side of IV; and those of the third the fibular side of IV and the tibial side of V. The accessory slip passes to the outer (fibular) side of the origin of *M. extensor brevis V* and there divides into two bundles, one of which inserts along the distal edge of tarsale 4 + 5, along the same line from which the latter muscle takes its origin, the other into the outer (fibular) side of the base of metatarsale V. This last slip thus completes on the fibular side of the fifth metatarsal the series of tendons that supply the lateral angles of the bases of the metatarsals and serve as ab- and ad-ductors of the set. The tibial side of digit II alone remains unsupplied from the femerometatarsalis system and the lack is supplied by a special abductor, the supinator, thus rendering the series complete.<sup>1)</sup>

*M. extensor tibialis (et)*. This is the very large mass of muscles which lies on the tibial side of the leg partly covered by the humerometacarpalis. After the removal of the latter it is seen to almost entirely cover the dorsal surface of the tibia and to extend at its proximal end so that it comes in contact with the extensor fibularis. It is divided into two portions, with origins in contact but with distinct insertions. The details are as follows:

a) *extensor tibialis superficialis (ets)*. This portion arises from along the distal margin of the tibial condyle of the femur. Almost as soon as the tibia is reached the deepest fibers of this portion begin to insert along its free margin and continue down the entire length of the bone. The remaining fibers pass under the margin of *M. supinator* and insert in two bundles, into the marginal and dorsal aspects of tibiale and tarsale II respectively. The most superficial of the fibers of this muscle are the longest, and consist of those that insert into tarsale II; beneath these lie the fibers that insert into the tibiale, and the deepest of all are those that insert into the tibia.

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1) For the treatment of this muscle by various authors cf. sub *M. humerometacarpalis*, the corresponding muscle in the arm.

b) *extensor tibialis profundus (etp)*. This portion lies medial to the former and is wholly covered by the *femorometatarsalis*. It arises from the distal margin of the distal epiphysis of the femur, about midway between the two condyles and directly beneath the origin of *M. femorometatarsalis*. This origin, tendinous at first, becomes muscular almost immediately and the fibers insert along the greater part of the fibular margin and over nearly the fibular half of the dorsal aspect of the tibia, including in length the most of its shaft.

This entire muscle, although in detail strikingly like its homolog in the forearm, differs from it in the absence of a nerve running between the two portions. What this failure may signify in the consideration of serial homology cannot of course be ascertained until the nerves of the two appendages have been thoroughly studied and homologised, but the nerve is not a very important one and its failure can hardly be considered as a serious obstacle to the homologisation of the tibial and radial extensors.

*M. supinator (s)*. This muscle is easily distinguished since it is the only one on the dorsal aspect of the limb that is obliquely placed. The terminal portion alone is superficial and may be seen emerging from beneath the *femorometatarsalis* upon the tibial side; the remainder is concealed by this latter muscle, which must be removed in order to expose it. It is a little larger than its homolog in the forearm, and extends as far as the fibula, from the distal tibial angle of which it possesses an origin. The two other origins are precisely as in the arm, viz: from the tibial margin and a bit of the dorsal surface of the *fibulointermedium*, and by a deeper slip from the *centrale*. The muscle is inserted by a tendon into the tibial margin of *metatarsale II*, near the base of the bone, and thus acts as an abductor of the digit, completing the system formed by the tendons of insertion of the *femorometatarsalis* and its accessory slip.

Owing to its mode of insertion this muscle has been designated by ST. JOHN BROOKS the "*extensor metatarsi hallucis*". HOFFMANN calls it *M. fibulae metatarsus II*. Its identity with the *supinator* of the anterior limb is beyond question.

*M. extensor fibularis (efb)*. This muscle occupies the outer (fibular) margin of the leg and is partly overlapped by the *femorometatarsalis*. It arises from the fibular condyle of the femur, and runs down over the dorsal aspect and free margin of the fibula. The more superficial and marginal fibers are the longest, and



enwrap and conceal the others, as described in the case of the ulnar extensor of the forearm. The insertion includes the entire free margin of the fibula, and is continued along the fibular margin of the fibulare-intermedium. A bundle of the shorter fibers covers the proximal part of the dorsal aspect of the fibula and forms an area of insertion that terminates in an oblique line across the middle of the shaft.

Mm. extensores breves (*eb* 2-5). These small muscles are four in number, one for each digit, and appear superficially as oval bellies, interdigitating with the slips of the femorometatarsalis. They arise from the distal margins of the tarsalia that correspond to the digits to which they belong, tarsale 4 + 5 giving rise to two, as would be expected. The bellies are continued into long, narrow tendons, but partially differentiated from the aponeurosis that covers the dorsal surface of the digits, and appear as thickened stripes along the middle of the toes. These insert into the bases of the terminal phalanges.

The relation of these short extensors and their partially differentiated tendons to the femorometatarsalis, and the possibility of the formation of an extensor communis from the union of both sets of muscles, has been fully discussed under the two muscles, humerometacarpalis and femorometatarsalis, and under the extensores breves of the arm.

## 2. Volar aspect of leg and foot.

Plantar fascia (*fp*). The muscles of the volar surface of the lower leg and foot are covered superficially by a fascia which, distal to about the middle of the leg, becomes thick and opaque, concealing all subjacent parts. This latter portion is the plantar fascia proper, and extends distally as a continuous sheet from the distal margin of *M. plantaris superficialis*, of which it forms an aponeurotic continuation. At about the base of the metatarsals it divides into four slips, which gradually narrow and lie along the volar aspects of the four digits, inserting into the bases of the terminal phalanges. These tendon-like slips are tied down by ligaments opposite the metatarso-phalangeal joints, and, in the case of digit IV, also opposite the extra joint between phalanges 1 and 2. While opposite the row of tarsalia, and shortly before its division into the four digital slips, the plantar fascia becomes firmly fastened to the distal border of these bones, and the crescentic partition of firm connective tissue thus formed, and the surface of the fascia



adjacent to it on the distal side, furnish the points of origin for the two sets of short flexors of the digits. Proximal to this partition the plantaris profundus becomes inserted into the dorsal (inner) surface of the fascia. The entire set of muscles thus united into a system through the medium of the plantar fascia includes both superficial and deep plantar muscles, as well as the two sets of short flexors, superficiales and profundi, and the whole system acts as a compound flexor of the digits.

As in the case of the corresponding fascia of the forearm and its similarly related muscles, there has been a general tendency to consider the system the equivalent of a long flexor, and the muscles have been frequently so named. The nomenclature adopted here is that of McMURRICH, 1903, in the forepaw of *Amblystoma*, the observations being made by means of serial sections. An equally recent author, OSAWA, who has described the condition in *Cryptobranchus*, refers to the entire system as *M. flexor digitorum (longus) sublimis*, the appellation "longus" being used only in the case of the forearm. It is likely that this difference in the use of names does not rest upon any marked differences in the species studied, but is due rather to the individual point of view, and emphasizes the fact that we have in the Urodeles the volar muscles at an interesting point in their differentiation from an indifferent volar mass to that of the long flexors characteristic of higher forms.

*M. plantaris superficialis (ps)*. This is a short, broad muscle, occupying the proximal half of the lower leg, and continued directly into the plantar fascia. It arises by fleshy fibers from the middle of the inner surface of the distal epiphysis of the femur, above (proximal to) the origin of *M. flexor tibialis*. From their origin the fibers diverge and form a broad belly, which inserts, when at its greatest breadth, into the proximal margin of the plantar fascia.

See notes to palmar and plantar fasciae, and to *M. palmaris superficialis*.

*M. plantaris profundus (pp)*. This is a large muscle-mass, which lies beneath the plantar fascia, and corresponds closely to its homolog in the hand. Like this it is divided into two masses by a longitudinal bundle, the fibulari-tarsalis, exactly as the palmaris profundus of the hand is divided by the ulnari-carpalis, but there are several minor points of difference in the area of origin. In both cases it is in the form of a line or narrow band, and here, as in the hand, this line runs down the shaft of the inner long bone and its corresponding tarsal (tibia and tibiale) but in the leg it does not become recurved and again cross the tibia, but runs over the

surface of the centrale instead (cf. Fig. 36 and 37). The muscle inserts in the form of two adjacent bundles into the dorsal (inner) surface of the plantar fascia, involving a large area.

*M. fibularitarsalis (fbt)*. This muscle consists of a long narrow band, running lengthwise through the mass of flexor muscles of the lower leg. It arises upon the flexor surface of the fibula, near its proximal end, almost continuous with the line of origin of the pronator. The band-like muscle, during its course, rests upon the last named, crossing it near its origin, with the fibers of the two muscles almost at right angles, and near its distal end parts the fibers of the plantaris profundus, to insert into the flexor surface of tarsale 4 + 5, near its distal margin, and thus adjacent to the points of origin of the *Mm. tarsometatarsalia*.

*M. flexor fibularis (ffb, rud. 1, rud. 2)*. This muscle, so large and well-developed in the anterior limb, is almost wanting in the foot, but seems to have left traces in the form of two very small muscles, the one extending from fibula to fibulare (Figs. 31, 33, *rud. 1*), the other from fibulare to tarsale 4 + 5 (Fig. 33 *rud. 2*). The insertions of these two rudiments correspond closely to those of the two bundles that form the longer mass of the flexor ulnaris (cf. Figs. 36 and 37), a significant point if it be taken into consideration that in the limb muscles the insertions, which are the distal attachments, are much more constant than the areas of origin, since the latter fluctuate with the extent of development, and thus vary with the size of the muscle, while the former, being the point at which the power is applied, cannot vary at all without modifying the physiological action of the whole muscle. The origins of these two rudiments are as close to the insertions as they can possibly be, the one from the distal margin of the fibula, the other from that of the fibulare. There is no suggestion of an origin from either the femur or the shaft of the fibula.

*M. flexor tibialis (ftb)*. This muscle, although forming a thin sheet, and easily overlooked, is still in evidence and clearly represents the flexor radialis of the anterior limb. It is nearly covered by the large pronator, and, as the two are similar sheet-like muscles and almost coincident, they are easily taken for a single one. It arises from the middle of the distal end of the femur, and is at first somewhat fusiform, but soon spreads out into a thin sheet, and inserts along an oblique line that runs across the distal third of the tibia and a part of the tibiale (Fig. 31); it thus

corresponds closely to its homolog in the arm, except that its area of insertion, in accord with the difference in the general form of the muscle, is somewhat different in shape (cf. Figs. 36 and 37, *fr* and *fb*).

*M. pronator (pr)*. This muscle, in position, direction, and use, corresponds closely to its homolog in the arm, but it is much broader at its origin. This area, in the form of a longitudinal line, includes nearly the entire length of the fibula and crosses almost the whole of the fibulointermedium, while that of its anterior homolog is confined to the middle part of the shaft of the ulna. It inserts by two slips, the one into the middle of the dorsal surface of tarsale 2, the other into the tibial side of the base of metatarsale II.

*Mm. flexores breves superficiales (fbs)*. Except, perhaps, in the detail of the bundles, which appear to be somewhat variable individually, I have found a complete correspondence between these small digital muscles and these of the same name in the hand. There are four slips, one for each digit, and they arise from the dorsal (inner) surface of the plantar fascia, that is, in part from the crescentic ligament that binds the latter to the tarsalia and in part from the fascia distal to this and proximal to the point at which the latter splits into the four slips destined for the four digits. Each of these four muscle masses is in itself compound, and is divisible into separate bundles, typically five in number, one median and, for each side of the digit, two lateral ones, exactly as in the hand. At the point of origin, in both foot and hand, these divisions are not always distinct, and the ultimate number may be reached, either by a primary division of the bundle into three, one for the middle and one for each side, the lateral ones dividing again, or else by a primary division into the five typical bundles. The first of these methods is shown in the illustrations of the hand, and the last in digit IV of the foot. Quite often, too, the median bundle seems to be continuous with the lateral one upon one side, making an apparent total of four, as is shown in digits II and III of the foot. These differences seem to be in part individual and in part due to the chance of dissection, as the separation of the slips at their origin is to some extent an artificial one although the insertions are definite. Attention may here be called to the precise correspondence of digit IV in hand and foot, even to the interpolation of the little interphalangeus in both (Figs. 34 and 35). The little fiber seen in Fig. 34 connecting the interphalangeus with

the deep flexor is an anomaly and in no way to be associated with the typical form of the muscle in either limb. I have found it but once, and have figured it as suggestive of the genetic relationship of the two muscles.

*Mm. flexores breves profundi (fbp)*. These four little digital slips are in all particulars precisely as in the hand, to the description of which, as well as to Figs. 30 and 31, the reader may be referred. The little cross slip, shown in Fig. 31, is not a constant feature but an anomalous one, and was included merely because the drawing was made from a camera sketch and represents an actual dissection. Whether there is any morphological significance in this or in other similar variations, I cannot say.

*M. flexor interphalangeus digiti quarti (fi)*. This minute slip is the same in both members. The separation of the muscle into two bundles, as figured in Fig. 37, is not usually as well-marked. The connection between this muscle and the deep flexor has been already commented upon (sub *fb*s in the foot and *fi* in the hand).

*Mm. tarsometatarsales (b, cd, ef, gh, those of the from digits respectively)*. These muscles correspond closely to the carpometacarpals of the hand, differing from them in only a few details:

Digit II. The outer (fibular) slip is more extensive, and spreads out to a longer line of insertion.

Digits III and IV. The two associated slips belonging to each digit are a little better developed than in the hand and are often confluent across the middle line of the digit, so that they may appear like a single sheet until they near their insertion.

Digit V. The outer (fibular) slip arises from the distal outer corner of the fibulare-intermedium; an origin from the tendon of a fibular flexor, as in the hand, is here impossible, owing to the reduced condition of this muscle.

*Mm. intermetatarsales (im 1—3)*. These small muscular sheets, which stretch across the three interosseous spaces, correspond exactly to those in the hand. They arise from the tibial, and insert into the fibular margins of the metatarsals.

*M. interosseus (io)*. This muscle is in the form of an oblique band, crossing the interspace between fibula and tibia and, strictly speaking located neither upon the extensor or the flexor side, but

in the same plane as the bones. Although physiologically either end may serve as origin, the more proximal, that is, the fibular, one, may serve as the anatomical origin, in accordance with the rule in the case of limb muscles.

This muscle is chiefly remarkable in having no serial homolog in the fore limb, and being thus the widest occurring departure from a complete correspondence between arm and leg.

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### Literature.

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- BROOKS, ST. JOHN, 1889, On the morphology of the Extensor muscles. Part I. Studies from the museum of Zoology in University College. Dundee, Vol. 1.
- DRÜNER, L., 1902, Studien zur Anatomie der Zungen-, Kiemenbogen- und Kehlkopfmuskulatur der Urodelen. I. Teil, in: Zool. Jahrb., Vol. 15, Anat.
- EISLER, P., 1895, Die Homologie der Extremitäten, in: Abh. naturforsch. Ges. Halle, Vol. 19.
- FÜRBRINGER, M., 1873, Zur vergleichenden Anatomie der Schultermuskeln, in: Morph. Jahrb., Vol. 1.
- HOFFMANN, C. K., 1873—1878, Amphibien, in: BRONN, Klass. Ordn. Tierreichs.
- HUMPHREY, G. M. 1872, The muscles and nerves of *Cryptobranchus japonicus*, in: Journ. Anat. and Physiol., Vol. 6.
- McMURRICH, G. P., 1903, The phylogeny of the forearm flexors, in: Amer. Journ. Anat., Vol. 2, No. 2.
- , 1903, The phylogeny of the palmar musculature, *ibid.*, No. 4.
- OSAWA, 1902, Beiträge zur Anatomie des japanischen Riesensalamanders, in: Mitt. Med. Facultät Kaiserl. Japan. Univ. Tokio, Vol. 5.
- RIBBING, L., 1907, Die distale Armmuskulatur der Amphibien, Reptilien und Säugetiere, in: Zool. Jahrb., Vol. 23, Heft 4.
- WILDER, HARRIS, H., 1903, The Skeletal system of *Necturus maculatus*, in: Mem. Boston Soc. Nat. Hist., Vol. 5, No. 9.
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### Explanation of the figures.

#### Plate 23—27.

- Fig. 1. Lateral view of shoulder region; superficial.
- Fig. 2. Similar to Fig. 1, but turned slightly towards the ventral side, and with the gills drawn away from the trunk muscles.
- Fig. 3. Lateral view of the shoulder-girdle, with the deeper muscles.
- Fig. 4. Inner (medial) surface of scapula, with muscle attachments.
- Fig. 5. Ventral view of the shoulder region; superficial.
- Fig. 6. Right shoulder-girdle and anterior appendage, with their muscles; detached from the body. Lateral view.
- Fig. 7. Right anterior appendage with a portion of the girdle, showing the muscles of the upper arm.
- Fig. 8. Same view as the preceding, with the muscles drawn apart.
- Fig. 9. Same view as the preceding, after removal of the superficial muscles.
- Fig. 10. Same view as the preceding. The deepest muscles.
- Fig. 11. Ventral view of hip girdle; superficial.
- Fig. 12. Same view as the preceding; a more advanced dissection. The left side is dissected farther than the right.
- Fig. 13. Ventral view of the hip girdle, with the deepest muscles; designed especially to show the puboischiofemoralis internus.
- Fig. 14. Inner (dorsal) aspect of the hip girdle, with limb.
- Fig. 15. Same view as the preceding; deeper muscles.
- Fig. 16. Lateral view of the hip girdle; skeleton.
- Fig. 17. Lateral view of the hip girdle, showing M. puboischiofemoralis internus.
- Fig. 18. Lateral view of the hip girdle; superficial.
- Fig. 19. Same view as the preceding; deeper muscles.

From this point on the Figures are given in pairs, representing corresponding views of the two limbs. The odd numbered figures, placed at the left of each pair, represent the anterior limb; the even numbers the posterior.

Figs. 20 and 21. Superficial views of the free limbs; extensor aspect.

Figs. 22 and 23. Same view as the preceding; deeper layer.

Figs. 24 and 25. Same view as the preceding; diagrams illustrating the origins and insertions of the muscles.!

Figs. 26 and 27. Superficial views of the free limbs; flexor aspect.

Figs. 28 and 29. Same view as the preceding; second layer.

Figs. 30 and 31. Same view as the preceding; third layer.

Figs. 32 and 33. Same view as the preceding; deep muscles.

Figs. 34 and 35. Details of digit IV; flexor aspect.

Figs. 36 and 37. Flexor aspect of the free limbs; diagrams illustrating the origins and insertions of the muscles.

The abbreviations used in the figures to designate the separate muscles are given in the list of the muscles at the beginning of the paper, and also accompany each name in the descriptive part. The separate digits are designated as II, III, IV and V, following the interpretation of HUXLEY, who assumes that the missing digit is the first. The separate bones do not require any explanation, except perhaps to recall the facts that in the carpus and tarsus the intermedium is fused with the outer bone of the proximal row, and that in the distal row the elements associated with the two last digits are also fused. The following abbreviations are used for muscles which do not appear in the text:

*la* levatores arcuum

*dl* dorsolaryngeus

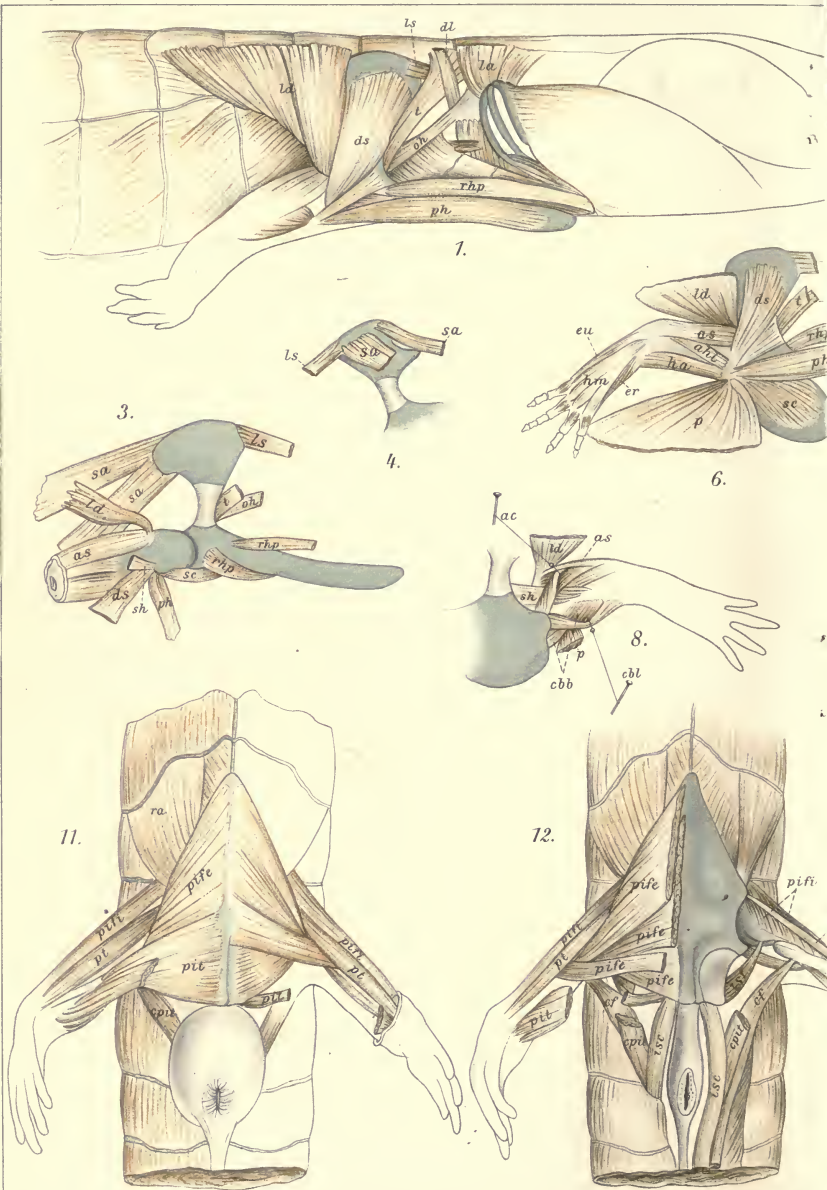
*ra* rectus abdominis.

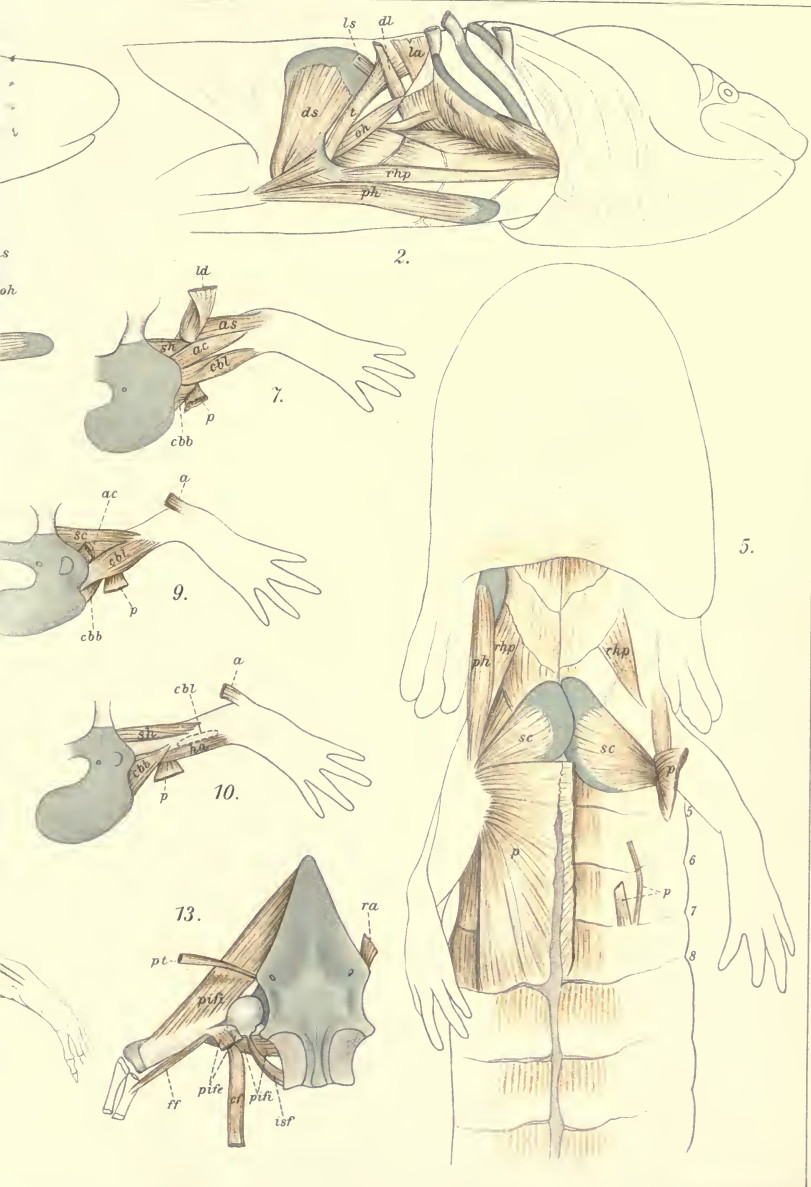








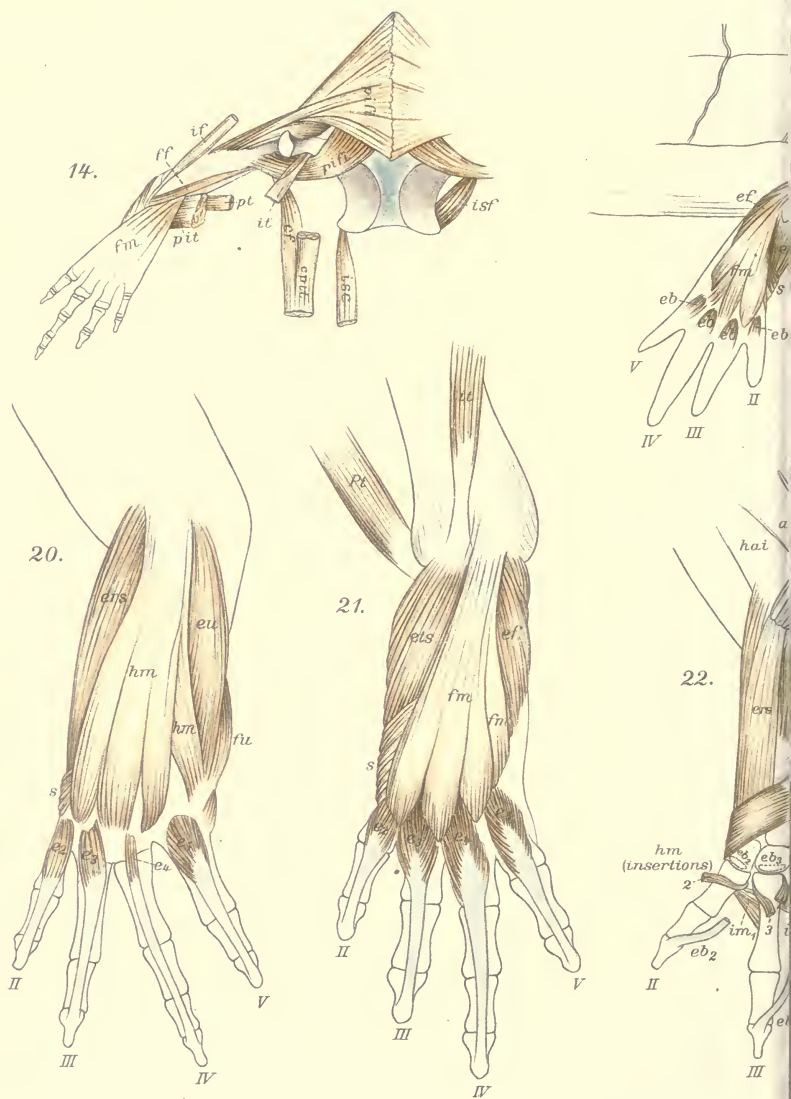


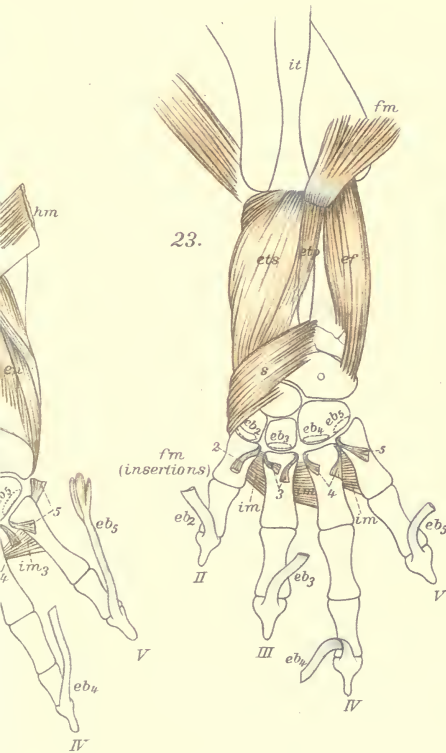
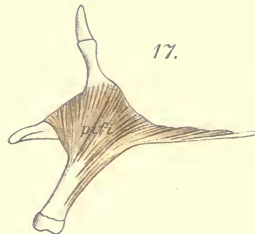
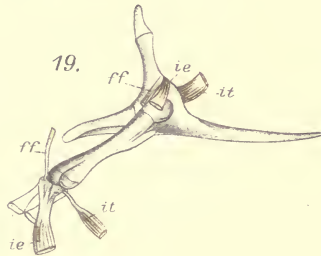
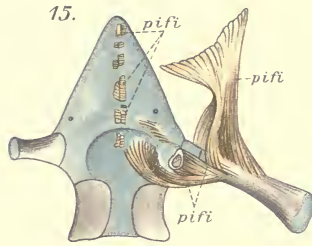
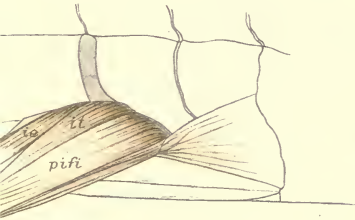










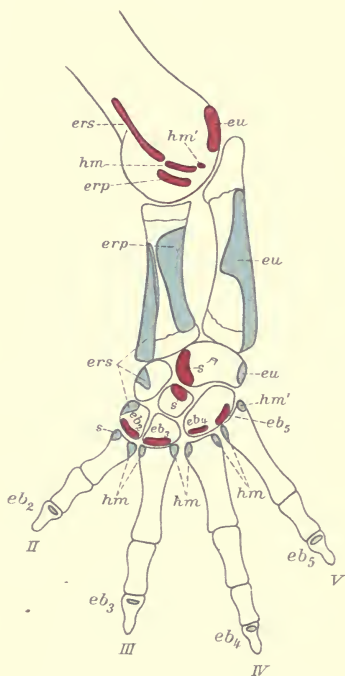




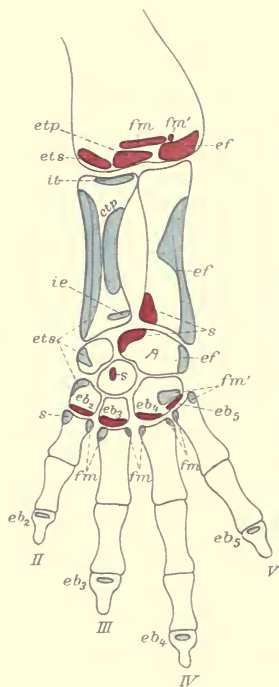




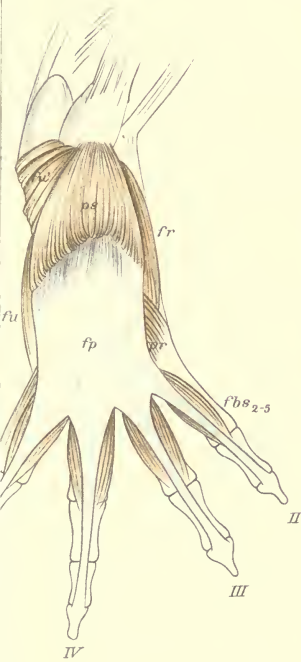
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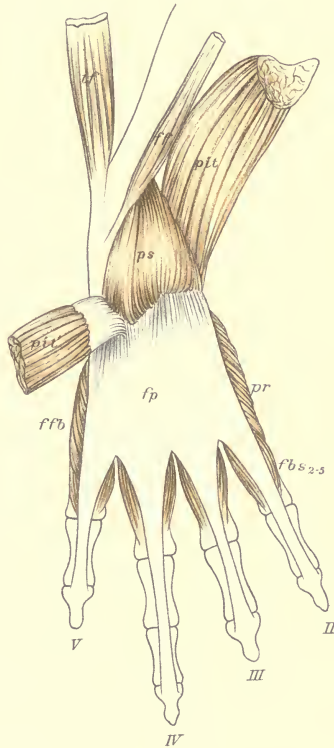
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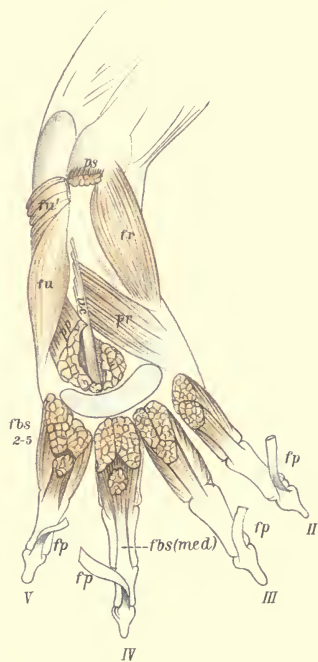




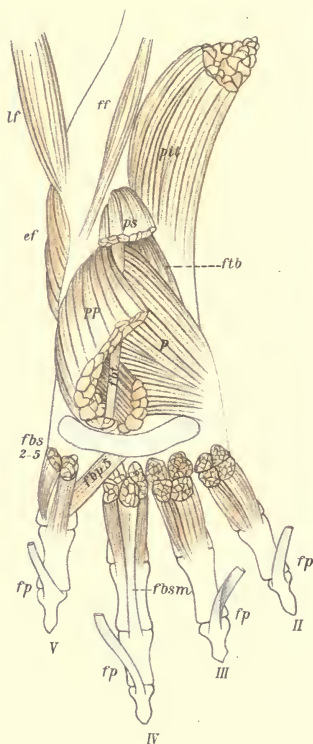




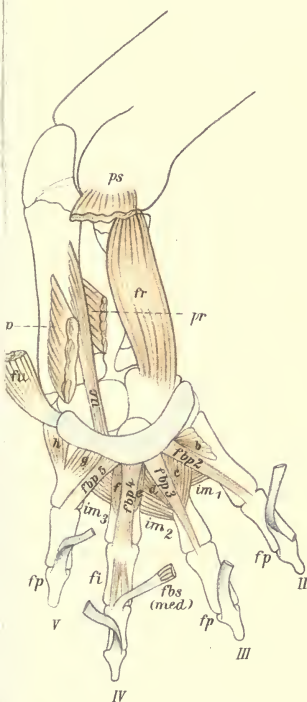
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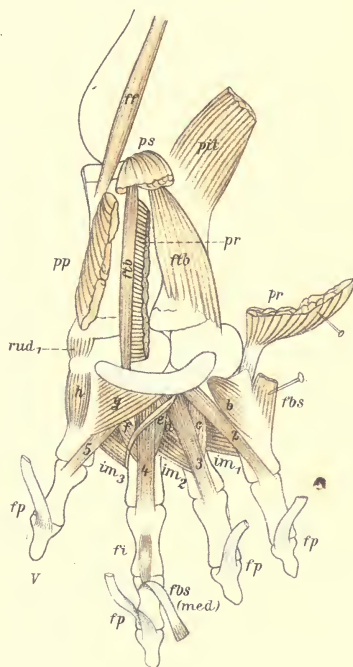
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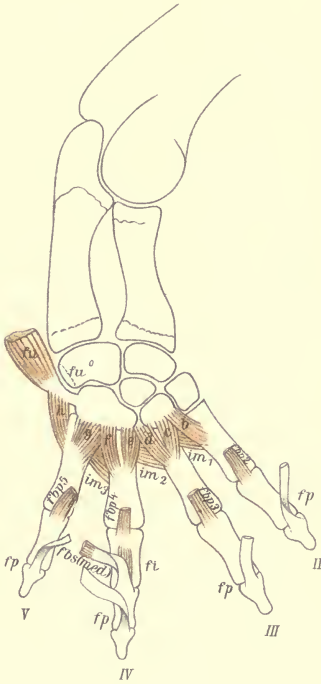




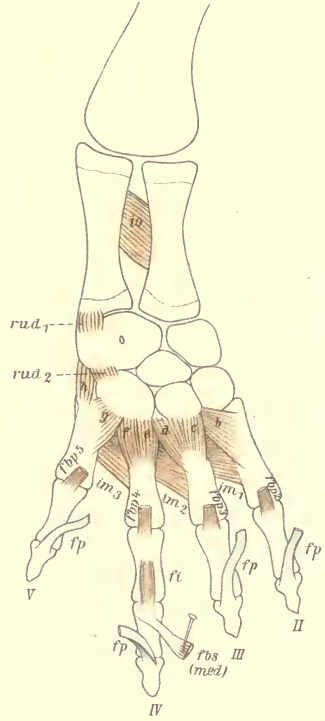




32.



33.





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Wilder, Harris Hawthorne

The appendicular muscles  
\* of *Necturus maculosus*.

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